Nutrient fluxes in litterfall and decomposition in four forests along a gradient of soil fertility in southern Ohio

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To determine how soil nutrient availability influences nutrient cycling, fluxes of nutrients through litterfall and decomposition were determined for four forest stands similar in all respects except soil nutrient availability and microclimate, within Neotoma Valley, a small watershed in southern Ohio, U.S.A. Litterfall varied from 10 to 60% among sites while nutrient concentrations and masses in new leaf litter varied as a function of extractable soil nutrient levels. Mass loss from litterbags was significantly higher in more fertile sites. Stepwise regression indicated that initial litter nitrogen and phosphorus concentrations were strongly correlated with relative decomposition rate while lignin concentration and microclimate variables were only correlated weakly. Thus, both litterfall nutrient transfers and decomposition rates were under the control of soil nutrient levels. Nitrogen was immobilized in litter at all sites during the 1st year of decay; litter from more fertile sites mineralized nitrogen during the 2nd year, while that from less fertile sites continued to immobilize nitrogen. Phosphorus and calcium mineralization rates were strongly correlated with the availability of these elements in the soil. Magnesium and potassium were leached rapidly from litter; amounts mineralized were correlated with amounts in litterfall. Interrelations among soil fertility, litterfall, and nutrient mineralization, as well as litter redistribution, are discussed as processes important in the development and maintenance of the soil fertility gradient in this watershed.

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Pour déterminer comment la disponibilité des éléments nutritifs du sol influence le cycle des éléments, l'auteur a mesuré les flux d'éléments accompagnant la chute et la décomposition de la litière dans quatre peuplements en tout point semblables, à l'exception de la disponibilité des éléments du sol et du microclimat. L'expérience a été conduite dans la Vallée Neotoma, un petit bassin du sud de l'Ohio, U.S.A. La chute de litière a varié de 10 à 60% entre les stations alors que les concentrations et les masses d'éléments dans la litière fraîche ont varié en fonction des niveaux d'éléments extractibles du sol. Les pertes de poids des sacs à litières étaient significativement plus élevées dans les stations les plus fertiles. L'analyse par régression progressive a indiqué que le taux de décomposition était fortement corrélé aux concentrations initiales d'azote et de phosphore de la litière, et relativement peu corrélé à la teneur en lignine de la litière et au microclimat. Conséquemment, le niveau d'éléments disponibles du sol influence l'importance des transferts d'éléments par la chute de litière et la minéralisation de la litière. L'azote fut immobilisé dans la litière dans toutes les stations au cours de la 1ʳᵉ année de décomposition; la minéralisation s'est amorcée au cours de la 2ᵉ année dans les stations les plus fertiles, mais, dans les stations les moins fertiles, l'immobilisation s'est poursuivie. Les taux de minéralisation du phosphore et du calcium étaient fortement corrélés à la disponibilité de ces éléments dans le sol. Le magnésium et le potassium furent lessivés rapidement de la litière; les quantités minéralisées étaient corrélées aux quantités initiales de ces éléments dans la litière. L'article traite aussi des interrelations entre la fertilité du sol, la chute de litière et la minéralisation des éléments, de même que de la redistribution de litière, comme processus importants dans le développement et le maintien du gradient de fertilité du sol dans ce bassin de drainage.

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Introduction

Valley watersheds of the unglaciated Allegheny and Cumberland Plateau regions of eastern North America have long been recognized to be mosaics of forest types (Sampson 1930; Wolfe *et al.* 1949; Braun 1950). Combinations of slope, aspect, and elevation generate patterns of microclimate which have been assumed to be major factors in determining forest species composition and relative abundances (Wolfe *et al.* 1949; Whittaker 1956; Mowbray and Oosting 1968).

In recent years, patterns of soil morphology and chemistry in these valleys have received increased attention. Strong gradients in soil conditions exist, even where parent materials are uniform. In general, soil pH and nutrient availability are lowest on ridgetops, intermediate to south- and west-facing slopes, and highest on north- and east-facing slopes (Finney *et al.* 1962; Franzmeier *et al.* 1969; Losche *et al.* 1970).

This gradient in soil fertility is influenced by the overlying forest vegetation, particularly through the pathways of litterfall

and decay, and also influences the vegetation through the effects of nutrient and moisture availability on growth. To understand these vegetation–soil interactions more clearly, this study has examined the nutrient fluxes through litterfall and decomposition in four forest stands which differ strongly in soil nutrient availability, in southern Ohio. In addition, the relative importance of litter quality (nutrient and lignin concentrations) and microclimate in determining the relative decay rate and nutrient mineralization was determined.

Methods

Study area

Neotoma Valley is a 73-ha watershed on the unglaciated Allegheny Plateau of southern Ohio, U.S.A. (latitude 39°35′ N, longitude 82°33′ W). The climate of Neotoma is temperate, cool, continental with an annual temperature maximum of 36°C, a minimum temperature of −25°C, and an annual precipitation of 100–105 cm (Wolfe *et al.* 1949).

Study sites were established in the four major forest types found in the valley: chestnut oak forest on the ridgetop, mixed oak forest on the southwest-facing slope, mixed mesophytic forest on the lower,

TABLE 1. Species composition of four forest study sites in Neotoma Valley, Ohio

	Sites			
Species	Chestnut oak	Mixed oak	Mixed mesophytic	Transitional
Quercus prinus	66.5	23.4	2.7	24.9
Acer rubrum	28.0	23.1	3.9	17.7
Fagus grandifolia	1.3	8.2	17.5	9.5
Quercus coccinea	—	21.1	—	—
Quercus alba	—	11.4	16.1	8.8
Nyssa sylvatica	—	5.1	5.0	12.4
Prunus serotina	—	—	16.5	—
Liriodendron tulipifera	—	—	18.3	14.6
Quercus borealis	—	—	14.8	1.8
Slope (°)	<5	15−25	20−25	25−35
Aspect (°)	—	230	50	50
Basal area and (standard error) (m²/ha)	36.4 (6.1)	32.4 (2.9)	33.4 (5.3)	30.5 (2.3)

NOTE: Importances percentages (IP) are the mean of relative density and relative basal area in six 10 × 10 m plots per site. Only species with IP greater than 10 in at least one study site are given; 47 tree species occur in the valley.

northeast-facing slope and transitional, red maple-tulip-chestnut oak forest on the mid-upper, northeast-facing slope (Fig. 1, Table 1). The four study sites are located in areas uncut since the mid-late 1800's.

Field methods

Six 0.5-m² litter traps were randomly placed within each study site. This replication was sufficient to obtain standard errors of the litterfall means of approximately 5% of the means. Litter traps were constructed of 6-mm hardware cloth, had 20 cm tall sides, and were placed 10−30 cm above the forest floor on steel posts. Litter was collected at weekly intervals during autumn (1 September − 15 December) and biweekly during the remainder of the year.

During October of 1980 and 1981, freshly fallen litter was collected at each site for litterbag incubations. After drying indoors for 2 weeks, the litter was sorted by species. Subsamples were dried at 80°C to determine initial dry weight of the litter subsequently packed in litterbags. Approximately 10 g of air-dried litter of representative species composition was placed in each 20 × 20 cm, 3-mm mesh polyethylene litterbag (Gosz *et al.* 1973; Lousier and Parkinson 1978). Chestnut oak site litterbags were packed with 9:1 *Quercus prinus* − *Acer rubrum* litter (mass basis), mixed oak site litterbags with equal amounts of *Q. alba, Q. coccinea, Q. prinus*, and *A. rubrum*, mesophytic site litterbags with 2:1:1:1 *Fagus − A. rubrum − Liriodendron − Q. alba* litter, and transitional site litterbags with 3:3:2 *A. rubrum − Q. prinus − Liriodendron* litter, respectively. Litterbags were returned to the study sites on 15 November 1980 and 1981. Three bags were recovered from each site at intervals of 1, 3, 5, 7, and 10 months, for both the 1980 and 1981 sets, and 15, 18, and 21 months for the 1980 set. Five bags per site were recovered at 12 (both sets) and 24 months (1980 set only). Recovered litterbags were weighed fresh, then dried at 80°C for 48 h before reweighing and grinding. Litter moisture was calculated as the difference between fresh and dry mass of litter in litterbags, taken during 15 dates over the 2 years. Soil moisture was determined in six samples per site taken on each of six dates during each growing season.

Precipitation volume was measured biweekly in three Taylor Clear-Vu rain gauges positioned in a 30 m wide pipeline right-of-way (Fig. 1). Estimates of actual evapotranspiration were made using the potential evapotranspiration tables of Thornthwaite and Mather (1957), actual precipitation and soil moisture measurements, and long term temperature profiles given by Wolfe *et al.* (1949).

Chemical and statistical analyses

Dried litter samples were ground in a Wiley mill with a 20-mesh screen, then ashed at 475−500°C for 4 h. The ash was then dissolved
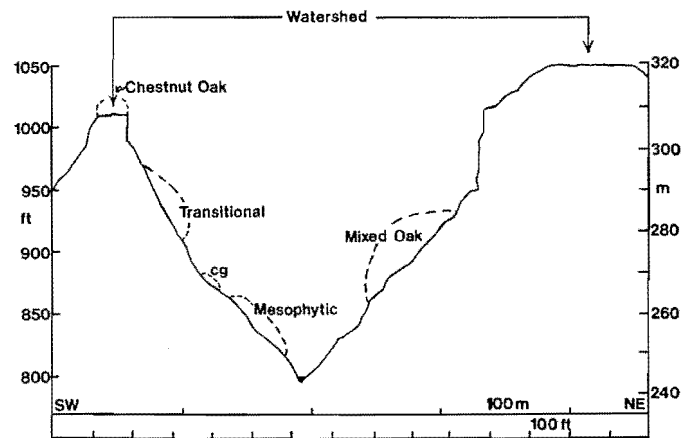

FIG. 1. Cross section of Neotoma Valley, Ohio, showing locations of study sites and the right-of-way (*cg*) in which rainfall collectors were positioned. 1 ft = 0.3048 m.

in 10 mL of 6N HCl (Likens and Bormann 1970) and brought to a volume of 100 mL. Phosphorus concentrations of litter digestate were determined by the stannous chloride method (Anonymous 1976). Following addition of La_2O_3 in 6N HCl (Likens and Bormann 1970), cation concentrations were determined by atomic absorption. Standard reference material (National Bureau of Standards 1575, red pine needles) was analyzed with each set of samples.

Nitrogen and lignin determinations were performed at the Ohio Agricultural Research and Development Center, Wooster, Ohio, utilizing semimicro-Kjeldahl (Bremner 1965) and Van Soest (1963) methods, respectively.

Soil samples were extracted with 2N KCl (for nitrogen forms) and NH_4OAc (for cations and phosphate), then analyzed as above.

Two approaches were used to analyzed mass loss from litterbags (Wieder and Lang 1982). First, the proportions of mass remaining were compared among sites and dates by two-way ANOVA. Then relative decay rates (*k*) (*sensu* Olson 1963) were estimated by non-linear regression of mass loss over time, and compared with possible correlated factors by stepwise regression. The Statistical Analysis System (Anonymous 1979) was used for analysis of variance, stepwise regression, and nonlinear regression to single and double exponential equations.

TABLE 2. Selected soil characteristics in four forest types in Neotoma Valley, Ohio, based on 12 samples per site. Soil names and textures follow Riemenschneider (1964)

| Site | Soil type | pH | Extractable nutrient concentration (μEq./100 g) | | | | | Base saturation (%) | Cation exchange capacity (mEq./100 g) |
			Nitrate	Phosphate	Calcium	Magnesium	Potassium		
Chestnut oak	Berk silt loam	3.7 a	26.2 a	87.2 a	457.4 a	144.0 a	69.5 a	3.0 a	21.7 a
Mixed oak	DeKalb fine sandy loam	4.0 a	33.3 a	192.1 a	831.7 a	268.8 a,b	76.3 a	7.8 b	15.3 b
Mesophytic	Neotoma fine sandy loam	4.7 b	48.8 b	361.6 b	1114.4 a	294.8 a,b	156.4 a,b	11.8 b	13.0 b
Transitional	Neotoma fine sandy loam	5.2 b	80.9 c	513.4 b	2985.7 b	481.3 b	181.6 b	35.6 c	11.3 b

NOTE: Values followed by the same lowercase letter were not significantly different at $p = 0.05$. Base saturations were arc sine transformed, and pH values converted to hydrogen ion concentrations, before analysis of variance.

TABLE 3. Leaf litterfall mass (grams per square metre) in four forest stands during 1981 and 1982. Standard errors of the means are given in parentheses

| Time period | Sites | | | |
	Chestnut oak	Mixed oak	Mesophytic	Transitional
1982 (full year)	331.5 (19.3) a	364.8 (11.6) a	385.8 (18.8) a	496.4 (15.1) b
Autumn 1981	355.2 (17.7)	428.5 (17.1)	367.3 (11.7)	457.7 (18.8)
Autumn 1982	310.4 (15.6)	341.5 (11.4)	357.6 (10.7)	468.5 (11.0)
1981−1982 difference	NS	$p < 0.01$	NS	NS

NOTE: Values followed by the same lowercase letter were not significantly different at $p = 0.05$.

Results

Microclimate and soil patterns

The soils of the study sites were all derived from the coarse-grained, Mississippian-age sandstones which underlay the valley (Wolfe et al. 1949; Riemenschneider 1964). All were fine sandy loams, except those of the chestnut oak stand which had slightly more silt and less very fine sand; all had <10% clay content (Riemenschneider 1964). Mean bulk density among sites ranged from 1.06 to 1.15 g/cm³ and field capacity from 16.6 to 19.0% by weight, though neither differed significantly among sites (Riemenschneider 1964).

Soil moisture varied between 15 and 35% by weight, depending on season and site. The patterns among sites paralleled those determined from weekly sampling of these sites over the period 1954−1961 by Laughlin and Gilbert (1962). The general pattern of soil moisture was mesophytic > transitional > chestnut oak > mixed oak, with differences on the order of 3−4% between sites. While differences among dates were significant following analysis of variance, neither site nor site × date interaction variances were significant. Thus seasonal differences in soil moisture were more important than intersite differences.

Estimated annual evapotranspiration (AET) volumes increased in the order transitional = mesophytic < chestnut oak = mixed oak in both years.

Soil chemistry varied considerably more than texture or moisture. A-horizon pH, base saturation, and extractable levels of major nutrients all increased in the following order: chestnut oak stand, mixed oak stand, mesophytic stand, transitional stand, including a threefold range in extractable nitrate and sixfold ranges in phosphate and calcium availability (Table 2). Thus while texture and exchange capacity were similar among the study sites, pH, base saturation, and nutrient availability all varied strongly and in a consistent pattern (Table 2).

Litterfall

The mass of leaf litterfall during 1982 varied from 332 g·m⁻²·year⁻¹ (chestnut oak site) to 496 g·m⁻²·year⁻¹ (transitional site) (Table 3). These values fall within the range for temperate deciduous forests of the region (Bray and Gorham 1964; Sharpe et al. 1980). Litterfall mass was significantly higher at the transitional site than at the other three sites (Table 3).

Over 90% of annual leaf litterfall occurred between 1 September and 15 December (Table 3). Rates of autumn leaf fall were similar in the 2 years except at the mixed oak site, where several treefalls occurred during April 1982. The removal of several large canopy trees from the immediate area of several littertraps resulted in 20% lower litterfall in autumn 1982 than in autumn 1981. While this change was statistically significant, it was well within established ranges of year-to-year variability in litterfall in deciduous forests (Bray and Gorham 1964).

While the total mass of leaf litterfall was not determined during autumn 1980, fresh litter was trapped that autumn for use in litterbags. Thus, nutrient concentrations in autumn leaf litter are available for 3 years (Table 4).

Nitrogen and phosphorus concentrations were consistent over the 3 years at each site, and varied directly with the extractable level of each in the soil (Table 4). Calcium and magnesium levels in litter correlated strongly with the availability of each in the soil during each year, but year-to-year differences in concentration weakened the overall 3-year pattern. The interyear differences in calcium and magnesium concentrations were similar in magnitude to those observed in other Appalachian deciduous forests (Day 1973).

Litter mass loss rates during decomposition

Mass losses over the 1st year of decay ranged from 30 to

TABLE 4. Mean nutrient concentrations in autumn leaf litterfall in four Ohio forests over 3 years

Site	Year	Nitrogen	Phosphorus	Calcium	Magnesium	Potassium
Chestnut oak	1980	0.733 (0.007) a	0.377 (0.017) a	8.250 (0.068) b	0.945 (0.014) a	4.293 (0.069) a
Mixed oak	1980	0.787 (0.003) b	0.463 (0.013) b	7.240 (0.100) a	0.941 (0.053) a	4.790 (0.100) b,c
Mesophytic	1980	0.893 (0.007) c	0.807 (0.020) c	12.282 (0.620) c	1.121 (0.059) b	4.535 (0.106) a,b
Transitional	1980	0.983 (0.058) c	1.293 (0.044) d	15.851 (0.391) d	1.992 (0.058) c	5.622 (0.283) c
		$r^2 = 0.943$	$r^2 = 0.957$	$r^2 = 0.815$	$r^2 = 0.842$	$r^2 = 0.467$
Chestnut oak	1981	0.697 (0.007) a	0.744 (0.094) b	7.106 (0.086) a	1.843 (0.032) a	5.079 (0.276) a
Mixed oak	1981	0.707 (0.009) a	0.554 (0.002) a	6.697 (0.222) a	1.870 (0.017) a	4.857 (0.399) a
Mesophytic	1981	0.863 (0.033) b	1.322 (0.114) c	8.160 (0.303) b	2.147 (0.110) b	5.282 (0.101) a
Transitional	1981	0.803 (0.045) b	1.227 (0.123) c	8.485 (0.137) b	2.073 (0.007) b	5.696 (1.315) a
		$r^2 = 0.400$	$r^2 = 0.654$	$r^2 = 0.605$	$r^2 = 0.425$	$r^2 = 0.813$
Chestnut oak	1982	0.729 (0.008) a	0.527 (0.023) a	8.442 (0.130) b	1.737 (0.066) a	3.985 (0.148) a
Mixed oak	1982	0.764 (0.021) a	0.495 (0.006) a	7.782 (0.074) a	1.670 (0.051) a	3.378 (0.152) a
Mesophytic	1982	0.900 (0.008) b	0.966 (0.020) b	11.576 (0.153) c	1.932 (0.099) a	4.988 (0.093) b
Transitional	1982	0.915 (0.015) b	1.150 (0.006) c	13.067 (0.166) d	1.985 (0.138) a	4.932 (0.117) b
		$r^2 = 0.766$	$r^2 = 0.917$	$r^2 = 0.714$	$r^2 = 0.853$	$r^2 = 0.827$
1980–1982		$r^2 = 0.598$	$r^2 = 0.760$	$r^2 = 0.438$	$r^2 = 0.215$ (NS)	$r^2 = 0.460$

NOTE: Standard errors of the means are given in parentheses. Within a sample year, values followed by the same lowercase letter were not significantly different at $p = 0.05$; r^2 values for regression against soil nutrient levels are given. All coefficients of determination were significant at $p = 0.05$ except those labelled (NS). Nitrogen values are in percent; other values are in milligrams per gram dry mass.

50%, with most of the loss occurring during the 1st month and during summer (Fig. 2). During each of the 2 years, mass loss rates were higher in the more fertile sites (transitional and mesophytic) than in the less fertile sites (chestnut oak and mixed oak). When the proportion of mass remaining on each of the six sampling dates during the 1st year of decay was compared among sites in a factorial ANOVA, the site and date differences were significant whereas the site × date interaction was not. Thus the patterns of mass loss among sites differed consistently throughout the initial year of decay in both 1980 and 1981 litterbag sets.

Second year mass losses ranged from 4.6 to 12.2% (Table 5). Because these low 2nd year mass losses were obscured by the effect of large differences in 1st year mass loss, the proportion of mass remaining at the end of 2 years was still significantly greater at the lower fertility sites (chestnut oak and mixed oak) than the more fertile sites (transitional and mesophytic) (Table 5).

When analyzed by nonlinear regression, patterns of mass loss from 1980 and 1981 litterbags, over the 1st year of decay, fit single exponential functions much better than double exponential or linear functions. The relative decay rates (k) were lower in the lower fertility sites than in the higher fertility sites during the 1st year of decay of each litter batch, and over the first 2 years of decay in the 1980 litter (Table 5). Rankings of decay rate show the same patterns as did the analysis of proportions of original mass remaining after 1 year.

Correlations of relative decay rates with environmental factors

Mass loss percentages and relative decomposition rates were compared with initial litter nitrogen, phosphorus, and lignin levels, litter and soil moisture, annual and summer (April–October) AET, and annual and summer rainfall in stepwise, multiple regressions. Because the results for mass loss percentages and k values were similar, only the regressions on k values will be presented. Extractable soil phosphorus and nitrogen levels were also included in the initial analysis. Because they correlated so strongly with initial litter concentrations (Table 4), however, they were deleted from the final regression matrix.

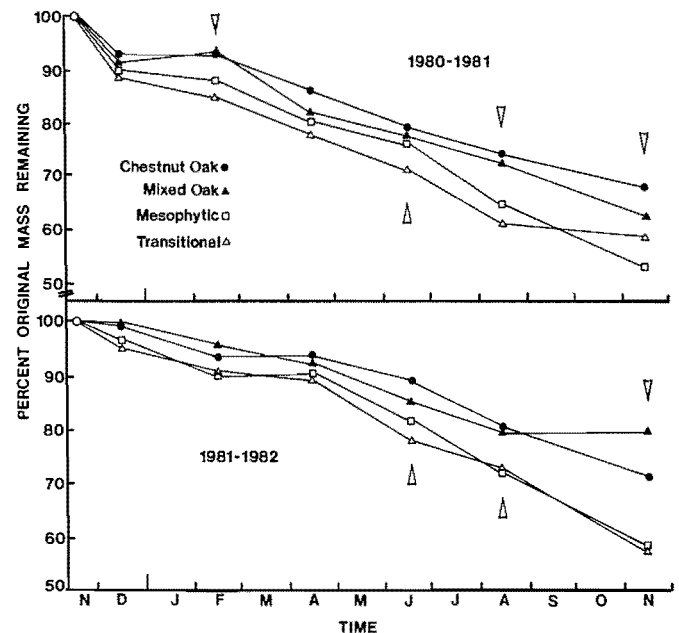The strongest single correlate to relative decay rate of the

FIG. 2. Mean mass loss from litterbags over 1 year of decay. Dates on which there were significant differences ($p = 0.05$) among sites are indicated by arrows.

litter was litter nitrogen concentration ($r^2 = 0.779$; $p < 0.001$); only litter nitrogen and phosphorus ($r^2 = 0.396$; $p < 0.01$) were significant single factor correlates to relative decay rate.

Lignin concentrations varied between 16.1% (Site O, 1981) and 20.7% (Site C, 1980) but did not correlate significantly ($r^2 = 0.143$) to k alone. When added to initial nitrogen, however, lignin concentration improved model fit to $r^2 = 0.859$. Nitrogen and phosphorus, together, resulted in $r^2 = 0.821$.

Microclimatic factors, such as AET and soil moisture, and lignin concentration have correlated well with decay rates on a broad scale (e.g., Meentemeyer 1978). On this narrower scale, where AET and lignin did not vary greatly among sites, initial litter nitrogen and phosphorus concentrations, which were dependant on the levels of these elements in the soil, correlated most strongly with decay rates.

TABLE 5. Proportion of mass remaining (percent mass), relative decomposition rate (k), and coefficients of determination (r^2) from nonlinear regression of mass losses from litterbags over 1 and 2 years

Parameters	Sites			
	Chestnut oak	Mixed oak	Mesophytic	Transitional
1980 litter (1st year)				
% mass	68.2 (2.9)	62.3 (4.6)	53.0 (1.7)	59.5 (5.6)
k	0.403 a	0.454 a	0.595 b	0.594 b
r^2	0.877	0.823	0.907	0.870
1981 litter (1st year)				
% mass	70.6 (2.1)	80.3 (7.5)	60.2 (3.8)	59.0 (2.0)
k	0.332 a	0.275 a	0.507 b	0.531 b
r^2	0.750	0.635	0.815	0.866
1980 litter (2 year net)				
% mass	63.9 (2.6)	57.7 (5.0)	40.8 (1.7)	49.4 (4.3)
k	0.238 a	0.290 a	0.437 b	0.442 b
r^2	0.648	0.707	0.888	0.753

NOTE: Standard errors of the estimates are given in parentheses. Rates followed by the same lowercase letter were not significantly different following pairwise t-tests using the standard error of the slope estimate from the nonlinear regressions.
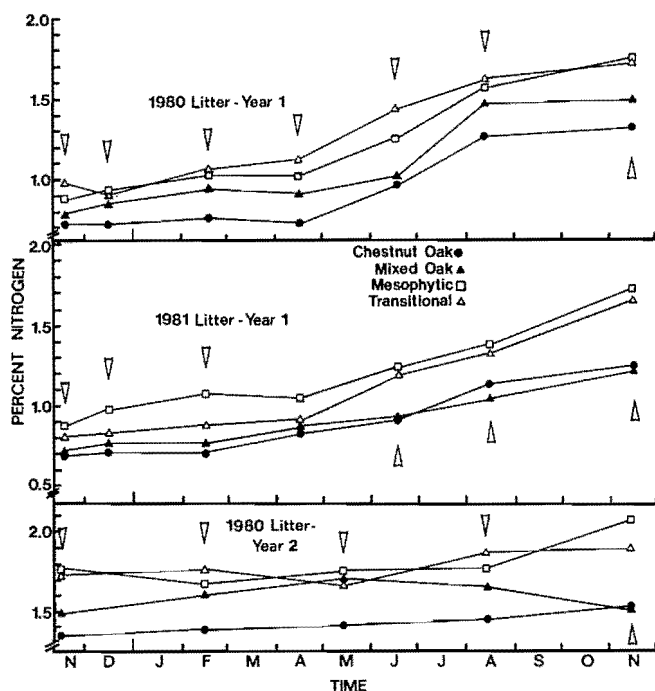

FIG. 3. Percent nitrogen in leaf litter during decay in four forest stands. Dates on which differences among sites were significant ($p = 0.05$) are indicated by arrows.

Litter nutrient mineralization—immobilization

Nitrogen

Nitrogen concentration increased significantly during the 1st year of decay in all sites and years (Fig. 3). Net immobilization of nitrogen mass in litter occurred in all sites (Table 6), even at the transitional and mesophytic sites, where mass loss was rapid. At the chestnut oak and mixed oak sites, the nitrogen mass in litterbags increased 18–25% (1980–1981) and 27–39% (1981–1982) during the 1st year of decay (Table 6). In contrast, the nitrogen mass present in litterbags in the transitional and mesophytic sites was not significantly different from the initial nitrogen mass (Table 6).

Litter nitrogen concentration increased throughout the 2nd year, though at lower rates, especially at the more fertile sites (Fig. 3). By the end of the 2nd year, 20–30% more nitrogen mass was present in the litter in the chestnut oak and mixed oak sites than at the time of litterfall. In contrast, net nitrogen mineralization began during the second summer at the transitional and mesophytic sites (Table 6).

Phosphorus

Phosphorus concentration in 1980 litter decreased in all sites during the first year of decay (Fig. 4). The differences among sites progressively decreased; the four sites' 1980 litter had similar phosphorus concentrations at the end of the 1st year (Fig. 4). By the end of the 1st year, 65–70% of the initial phosphorus mass had been mineralized in the more fertile sites, compared with 35–50% at the nutrient-poor sites (Table 6).

A decrease in phosphorus concentration also occurred in the 1981 litterbags through June of their 1st decay year. From then on, however, phosphorus concentration increased to levels equivalent to, or greater than, original levels (Fig. 4; Table 6), though the pattern of differences among sites observed in fresh litter persisted throughout the 1st year. As a result of this summer increase in phosphorus, net phosphorus mineralization was significantly lower in all sites during 1981–1982 than during 1980–1981 (Table 6).

Litter phosphorus concentration increased in all sites during the 2nd year of decay (Fig. 4). By the end of the 2nd year, differences in phosphorus concentration and mass among sites paralleled differences in A1 soil horizon levels. While significant interyear differences did occur in phosphorus dynamics, consistently higher rates of mineralization occurred in sites with higher soil phosphorus availability.

Calcium

Initial 1980 calcium litter concentrations were higher in the fertile sites than in the infertile sites (Fig. 5). Concentrations converged during the year; while differences among sites at the end of the year were significant, the range was less than half as large as the initial range (Fig. 5). Approximately 40–50% of initial litter calcium mass was mineralized at the fertile sites, compared with 23% at the chestnut oak site and <3% at the mixed oak site (Table 6).
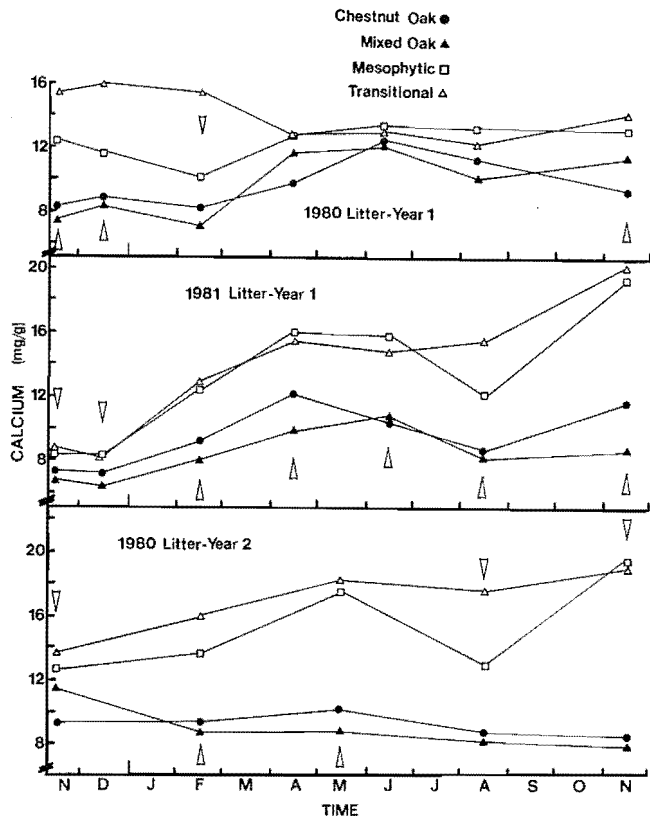
FIG. 4. Phosphorus concentration (milligrams per gram of dry mass) in leaf litter during decay in four forest stands. Dates on which differences among sites were significant ($p = 0.05$) are indicated by arrows.

In the infertile sites, where interyear differences in initial concentrations were small (chestnut oak, 13% and mixed oak, 4%), the 1981–1982 patterns of concentration changes were similar to the 1980–1981 patterns (Fig. 5), an increase through late spring then generally constant values through autumn. In the more fertile sites, initial calcium concentrations were significantly lower in 1981 than in 1980 (transitional site, 47% and mesophytic site, 33%), and calcium concentration rose throughout the year (Fig. 5). As a result, calcium was immobilized in those sites during 1981–1982 (Table 6). Calcium concentrations changed little during the 2nd year of decay (Fig. 5); as a result, calcium mineralization was proportional to mass loss (Tables 5 and 6).

During 1980–1981, the range and pattern of initial calcium concentrations paralleled those of soil calcium availability, and the patterns of calcium mineralization paralleled mass loss rates. In 1981–1982, a year in which initial calcium concentrations were lower at the fertile sites, and the intersite concentration range therefore smaller, calcium was immobilized in the more fertile sites, such that concentrations at the end of the 1st year more closely paralleled soil calcium availability. While patterns of calcium, phosphorus, and nitrogen mineralization–immobilization changed little from 1980–1981 to 1981–1982 at the chestnut oak and mixed oak site, lower rates of mineralization of all three elements occurred at the transitional and mesophytic sites 1981–1982 as compared with 1980–1981. This may, in part, be due to a very dry summer in 1982 when precipitation volume was only 41% of normal (compared with National Oceanographic and Atmospheric Administration esti-

TABLE 6. Mean percent original concentration and mass for five elements in leaf litter following 1 and 2 years of decay in four Ohio forest sites. Standard errors of the mass means are given in parentheses

Site	Nitrogen % original concentration	Nitrogen % original mass	Phosphorus % original concentration	Phosphorus % original mass	Calcium % original concentration	Calcium % original mass	Magnesium % original concentration	Magnesium % original mass	Potassium % original concentration	Potassium % original mass
1980 litter (1st year)										
Chestnut oak	183.3	124.6 (4.5)	97.9	64.3 (1.6)	112.5	76.7 (6.0)	83.2	57.8 (13.2)	17.2	11.8 (2.2)
Mixed oak	190.2	118.0 (6.4)	74.5	47.3 (10.8)	158.2	97.1 (6.7)	77.3	48.8 (3.7)	26.2	16.1 (2.8)
Mesophytic	198.7	108.0 (6.1)	51.9	27.5 (1.2)	104.9	55.8 (3.8)	90.4	48.1 (4.1)	32.9	17.7 (4.5)
Transitional	181.9	107.4 (5.9)	40.3	23.5 (2.5)	84.9	50.9 (6.9)	76.1	44.4 (0.6)	28.5	17.8 (2.4)
1981 litter (1st year)										
Chestnut oak	179.3	126.5 (4.2)	126.7	89.1 (2.0)	166.5	117.3 (2.7)	63.6	44.7 (3.2)	36.3	25.7 (1.2)
Mixed oak	172.6	138.7 (14.4)	147.8	122.5 (11.5)	128.9	104.4 (6.4)	56.1	46.9 (7.7)	26.0	22.6 (2.9)
Mesophytic	200.5	122.7 (11.3)	105.4	63.5 (3.3)	239.2	143.8 (9.2)	92.9	56.3 (5.7)	34.4	20.8 (1.5)
Transitional	208.0	122.0 (12.2)	123.5	72.5 (3.5)	236.6	139.3 (5.5)	88.5	55.2 (5.8)	34.8	20.5 (1.6)
1980 litter (2 year net)										
Chestnut oak	212.8	131.3 (6.3)	276.0	171.9 (11.3)	100.9	65.5 (7.9)	86.7	54.9 (4.5)	36.6	22.3 (1.8)
Mixed oak	191.9	120.7 (7.8)	255.4	150.0 (15.4)	109.4	68.7 (2.6)	87.6	48.4 (3.2)	33.2	19.7 (2.3)
Mesophytic	230.7	94.9 (3.3)	237.7	97.9 (11.5)	156.5	63.5 (1.9)	80.6	45.6 (4.3)	38.6	11.1 (3.7)
Transitional	193.3	96.3 (11.2)	107.7	53.8 (6.8)	117.0	58.2 (6.2)	82.3	40.5 (3.1)	31.1	15.2 (0.9)

TABLE 7. Nutrient mineralization (immobilization) during litter decay in four Ohio forest sites. Fluxes (milligrams per square metre per year) are the product of 1982 litterfall fluxes and the proportion of mass of each nutrient remaining at the end of 1 and 2 years of incubation in litterbags

| Site	Nitrogen	Phosphorus	Calcium	Magnesium	Potassium
1980 litter (1st year)					
Chestnut oak	(593)	69	627	234	1125
Mixed oak	(495)	90	79	304	1067
Mesophytic	(269)	276	1890	377	1537
Transitional	(282)	444	3063	541	1993
1980 litter (2nd year)					
Chestnut oak	(161)	(227)	302	16	(134)
Mixed oak	(74)	(176)	778	2	(46)
Mesophytic	441	(268)	(329)	18	123
Transitional	419	(350)	(455)	38	63
1980 litter (2 year net)					
Chestnut oak	(754)	(139)	929	250	991
Mixed oak	(569)	(85)	858	306	1021
Mesophytic	172	8	1604	395	1660
Transitional	141	326	2607	579	2056
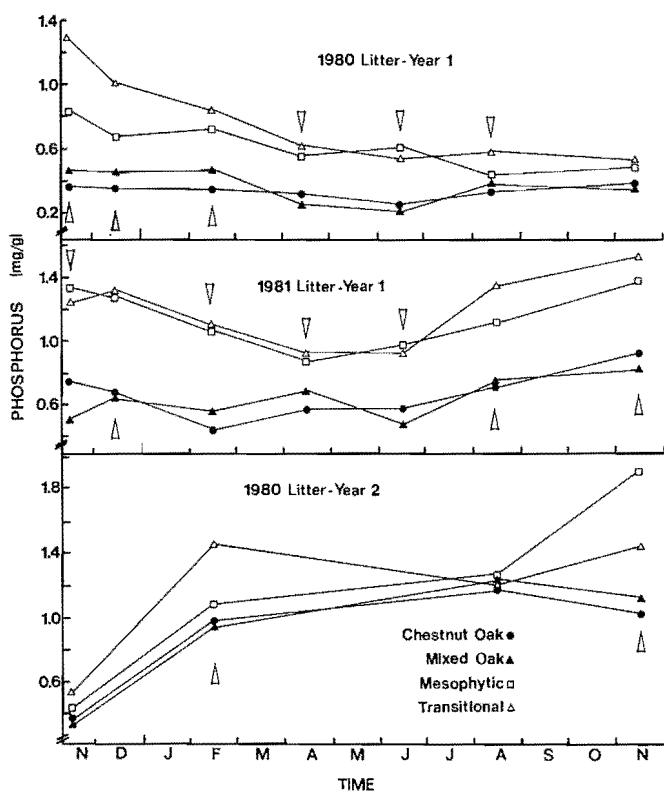
FIG. 5. Calcium concentration (milligrams per gram of dry mass) in leaf litter during decay in four forest stands. Dates on which differences among sites were significant ($p = 0.05$) are indicated by arrows.

mates), since soil biota at normally moister sites may be more sensitive to a drier-than-average summer than those in typically drier sites.

Magnesium and potassium

The concentrations of magnesium and potassium decreased rapidly in all sites during both years. By April–May of the 1st decay year, approximately half the original magnesium mass and 80% of the potassium mass had been lost. Little further loss occurred through the remainder of the 1st year in either 1980 or 1981, or during the 2nd year in 1980 litterbags (Table 6).

There were no significant site, year, or site × year differences in magnesium or potassium losses.

Net fluxes during decomposition

Actual fluxes of nutrients from litter to A1 horizons were estimated by multiplying the proportion of original mass of each nutrient mineralized or immobilized per year from 1980 litterbags by the amount of that element in leaf litterfall (Table 7).

Net immobilization of nitrogen occurred in all sites in 1st-year litter, though net immobilization was two- to three-fold higher in the less fertile sites. During the 2nd year of decay, litter in the less fertile chestnut oak and mixed oak sites continued to immobilize nitrogen, though at a lower rate, while rapid mineralization occurred in the more fertile sites (Table 7). Phosphorus was mineralized rapidly in the more fertile sites during the 1st year as well, while mineralization in the less fertile sites was three to five times slower. Net phosphorus immobilization occurred in litter during the 2nd year in all sites. Over a 2-year period, litter from the chestnut oak and mixed oak sites was a sink for nitrogen and phosphorus, while litter in the transitional and mesophytic sites served as a net source (Table 7).

Two-year net mineralization of calcium, magnesium, and potassium increased in the following order: chestnut oak < mixed oak < mesophytic < transitional (Table 7). For calcium, this was a result of more rapid 1st-year mineralization in the fertile sites, while for magnesium and potassium it reflected higher inputs in fresh litterfall.

Stand basal area, microclimate, and soil conditions may all affect rates of litterfall and decomposition. In these four stands of similar basal area (Table 1), masses of nutrients in standing litter and fresh litterfall increased with increasing soil fertility. Mass loss rates and nutrient mineralization rates from leaf litter also correlated well with soil nutrient levels but poorly with microclimate and lignin concentration. Thus, soil fertility was the single most important factor in influencing nutrient cycling through litterfall and decomposition in these four forests.

Discussion

The patterns of soil morphology and chemistry of unglaciated Allegheny and Cumberland Plateau valley watersheds

are as striking as the patterns of forest composition. South- and west-facing slopes are generally warmer, especially in winter, and have deeper, more heavily weathered soils (Finney *et al.* 1962; Franzmeier *et al.* 1969; Losche *et al.* 1970; Hutchins *et al.* 1976). In areas where parent materials are similar among sites, north- and east-facing slopes have higher soil organic matter content, higher pH, higher base saturation, and more extractable nitrogen than south- and west-facing slopes (Franzmeier *et al.* 1969; Hutchins *et al.* 1976). These patterns were also found in Neotoma Valley (Table 2). The presence of forests with contrasting species composition on slopes of different microclimate and soil fertility suggests two general areas for discussion. First, how do these patterns of soil fertility develop, and second, how do they affect ecosystem functional processes, such as litterfall and decomposition.

If weathering rates on warmer slopes are higher, and erosion and leaching more pronounced (see Losche *et al.* 1970; Hutchins *et al.* 1976), soils on southwest-facing slopes should be lower in available base cations, as was the case in Neotoma Valley (Table 2). However, differences in throughfall volume (R. E. J. Boerner, unpublished data) and soil temperatures (Wolfe *et al.* 1949) in Neotoma Valley are small and seem insufficient to explain the large variation in fertility.

Franzmeier *et al.* (1969) and Hutchins *et al.* (1976) noted higher organic matter content and nutrient availability on north- and northeast-facing slopes. Franzmeier *et al.* (1969) suggested slower decomposition as a cause, though my data showed higher rates of decomposition on the northeast-facing slope.

Franzmeier *et al.* (1969) also suggest downslope redistribution of litter as a potentially important mechanism in maintaining the fertility gradient. Significant downslope litter redistribution has been demonstrated in similar watersheds (Orndorff and Lang 1981; Lang and Orndorff 1984) and suggested for Neotoma (Wolfe *et al.* 1949). In Neotoma, the ratio of annual litterfall to annual change in litter standing mass (November maximum − August minimum) in 1981 was >1 at the mesophytic and transitional sites, indicating a subsidy of litter from elsewhere, presumably upslope, and <1 at the chestnut oak and mixed oak sites, indicating a net loss of litter to redistribution (R. E. J. Boerner, unpublished data). Welbourn *et al.* (1981) have shown such redistribution to be important in New York forests, with the amount of redistribution correlating with available soil calcium and organic matter. The relatively greater redistribution suggested for the southwest-facing slope at Neotoma may be related to differences in litter compaction, litter moisture retention, or wind patterns (Franzmeier *et al.* 1969; Welbourn *et al.* 1981; Orndorff and Lang 1981; Lang and Orndorff 1984). We are currently quantifying the rates of downslope redistribution in this watershed.

The gradients of soil fertility may originate through interactions of microclimate and parent material weathering. The fertility gradient may interact with microclimate to influence tree species composition and abundance through effects on seedling establishment and success (Racine 1971) and growth rates (Mowbray and Oosting 1968). Finally, interactions among vegetation, microclimate, topography, and soil nutrient availability may maintain, and perhaps enhance, the gradient of fertility. Boerner (1984) found that trees growing in the mixed oak stand had lower maximum foliar nitrogen and phosphorus concentrations, and resorbed a larger proportion of N and P prior to litterfall, than did individuals of the same species in the mesophytic site. Thus, trees were more conser-

vative of nutrients in the nutrient-poor site, and as a result, produced nutrient-poor litter. The nutrient dynamics occurring during decay of relatively nutrient-rich litter in the mesophytic site, and nutrient-poor litter in the mixed oak site, will help maintain, or even increase, the fertility differences between these sites.

A second area of investigation involves the effect of these patterns of soil fertility on ecosystem processes, such as litter decomposition. In general, the rate at which mass is lost from leaf litter is regulated by microclimate, especially litter−soil moisture (Witkamp and Van der Drift 1961) or AET (Meentemeyer 1978), and litter quality. As measures of litter quality, lignin content (Fogel and Cromack 1977; Meentemeyer 1978), carbon−element ratios (Gosz *et al.* 1973), and combinations thereof (Herman *et al.* 1977) have all been shown to correlate with mass loss and nutrient mineralization rates. Estimated AET and lignin content did not vary widely among the four forest stands in Neotoma Valley, and were not significantly correlated with mass loss or nutrient mineralization. Initial nutrient concentrations in litterfall, which correlated well with mass and nutrient loss rates, in turn, were related to soil nutrient levels in Neotoma Valley sites, and in other studies (e.g., Stachurski and Zimka 1975; Miller *et al.* 1976). Thus, along a gradient of soil fertility, where microclimate and lignin varied less than fertility, soil nutrient availability was the major controller of fluxes of nutrients in litterfall, and mass−nutrient fluxes during decomposition.

Whole-watershed nutrient budgets for a valley such as Neotoma can be calculated as the difference between inputs from weathering and bulk precipitation, and outputs in stream flow. Such budgets, however, give little insight into the dynamics of much of the watershed. The interaction of litter redistribution among forest stands (Orndorff and Lang 1981; Lang and Orndorff 1984) and the nutrient dynamics in litterfall and decomposition documented here, suggest that some parts of Neotoma Valley, such as the narrow floodplain and the moister, more fertile northeast-facing slope have high soil nutrient availability, subsidies of litter organic matter and nutrients, and are net mineralizers of nitrogen and phosphorus. Coversely, ridgetop and southwest-facing slope stands have lower soil nutrient availability, are net exporters of organic matter, and immobilize nitrogen and phosphorus from precipitation and the soil solution. More snowmelt and soil water flow enter the drainage stream from the northeast-facing slope. The chemistry of the drainage stream may be more reflective, therefore, of the forest floor−soil dynamics of the nearby, mineralizing stands than those farther from the streambanks (c.f. Lang and Orndorff 1984). Thus, whole-watershed budgets may represent valid means of all the forest stands in the valley while differing significantly from the budget of any of them. Before whole-watershed estimates are used to predict the impacts of disturbances or management strategies on single forest stands within Appalachian plateau valleys, the degree to which those estimates reflect rates and patterns of nutrient cycling in that stand, and the potential effect on downslope stands, should be evaluated.

Acknowledgements

ANONYMOUS. 1976. American Public Health Association. Standard methods for the examination of water and wastewater. 14th ed. American Public Health Association, Washington, DC.

ANONYMOUS. 1979. Statistical analysis system. S.A.S. user's guide. 1979 ed. S.A.S. Institute, Inc., Raleigh, NC.

BOERNER, R. E. J. 1984. Foliar nutrient dynamics and nutrient use efficiency in four forest tree species in relation to soil fertility. J. Appl. Ecol. 21(3). In press.

BRAUN, E. L. 1950. Deciduous forests of eastern North America. Blakiston Press, Philadelphia.

BRAY, J. R., and E. GORHAM. 1964. Litter production in forests of the world. Adv. Ecol. Res. 2: 101–157.

BREMNER, J. M. 1965. Inorganic forms of nitrogen. In Methods of soil analysis, part 2. American Society of Agronomy, Madison, WI. pp. 1179–1237.

DAY, F. P., JR. 1973. Primary production and nutrient pools in the vegetation on a southern Appalachian watershed. Ph.D. dissertation, University of Georgia, Athens, GA.

FINNEY, H. R., N. HOLOWACHUK, and M. R. HIDDLESON. 1962. The influence of microclimate on the morphology of certain soils of the Allegheny Plateau of Ohio. Soil Sci. Soc. Am. Proc. 26: 287–292.

FOGEL, R., and K. CROMACK, JR. 1977. Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. Can. J. Bot. 55: 1632–1640.

FRANZMEIER, D. P., E. J. PEDERSEN, T. J. LONGWELL, J. G. BYRNE, and C. K. LOSCHE. 1969. Properties of some soils in the Cumberland Plateau as related to slope aspect and position. Soil Sci. Soc. Am. Proc. 33: 755–761.

GOSZ, J. R., G. E. LIKENS, and F. H. BORMANN. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Experimental Forest, N.H. Ecol. Monogr. 43: 173–191.

HERMAN, W. A., W. B. MCGILL, and J. F. DORMAR. 1977. Effects of initial chemical composition on decomposition of roots of three grass species. Can. J. Soil Sci. 57: 205–215.

HUTCHINS, R. B., R. L. BLEVINS, J. D. HILL, and E. H. WHITE. 1976. Influence of soils and microclimate on vegetation of forested slopes in eastern Kentucky. Soil Sci. 121: 234–241.

LANG, G. E., and K. A. ORNDORFF. 1984. Surface litter, soil organic matter, and the chemistry of mineral soils and foliar tissue: landscape patterns in forests located on mountainous terrain in West Virginia. Proceedings of the Fourth Central Hardwood Forest Conference, University of Kentucky, Lexington, KY. In press.

LAUGHLIN, R. L., and G. E. GILBERT. 1962. Neotoma weekly soil moisture data, 1955–1961. The Neotoma Ecological and Bioclimatic Laboratory, The Ohio State University, Columbus, Ohio. Supplement No. 3.

LIKENS, G. E., and F. H. BORMANN. 1970. Chemical analysis of plant tissues from the Hubbard Brook Ecosystem in New Hampshire. Yale Univ. For. Bull. 79.

LOSCHE, E. K., R. J. MCCRACKEN, and C. B. DAVEY. 1970. Soils of steeply sloping landscapes in southern Appalachian mountains. Soil Sci. Soc. Am. Proc. 34: 473–478.

LOUSIER, J. D., and D. PARKINSON. 1978. Chemical element dynamics in decomposing leaf litter. Can. J. Bot. 56: 2795–2812.

MEENTEMEYER, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology, 59: 465–472.

MILLER, H. G., J. M. COOPER, and J. D. MILLER. 1976. Effect of nitrogen supply on nutrients in litterfall and crown leaching in a stand of Corsican pine. J. Appl. Ecol. 13: 233–248.

MOWBRAY, T. B., and H. J. OOSTING. 1968. Vegetational gradients in relation to environment and phenology in a Southern Blue Ridge gorge. Ecol. Monogr. 38: 309–344.

OLSON, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology, 43: 322–331.

ORNDORFF, K. A., and G. E. LANG. 1981. Leaf litter redistribution in a West Virginia hardwood forest. J. Ecol. 69: 225–235.

RACINE, C. H. 1971. Reproduction of three species of oaks in relation to the vegetational and environmental gradients in the southern Blue Ridge. Bull. Torrey Bot. Club, 98: 297–310.

RIEMENSCHNEIDER, V. L. 1964. Soils of Neotoma. Part II of the final report to the AEC of research contract AT (11-1)-552. The Neotoma Ecological and Bioclimatic Laboratory, The Ohio State University, Columbus, OH.

SAMPSON, H. C. 1930. The mixed mesophytic forest community of northeastern Ohio. Ohio J. Sci. 30: 358–367.

SHARPE, D. M., K. CROMACK, JR., W. C. JOHNSON, and B. S. AUSMUS. 1980. A regional approach to litter dynamics in southern Appalachian forests. Can. J. For. Res. 10: 395–404.

STACHURSKI, A., and J. R. ZIMKA. 1975. Methods of studying forest ecosystems: leaf area, leaf production and withdrawal of nutrients from leaves of trees. Ekol. Pol. 23: 637–648.

THORNTHWAITE, C. W., and J. R. MATHER. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Drexel University, Philadelphia, PA. Publ. Climatol. 10(3): 1–311.

VAN SOEST, P. J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. J. Assoc. Off. Anal. Chem. 49: 546–551.

WELBOURN, M. L., E. L. STONE, and J. P. LASSOIE. 1981. Distribution of net litter inputs with respect to slope position and wind direction. For. Sci. 27: 651–659.

WHITTAKER, R. H. 1956. Vegetation of Great Smokey Mountains. Ecol. Monogr. 26: 1–80.

WIEDER, R. K., and G. E. LANG. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology, 63: 1636–1642.

WITKAMP, M., and J. VAN DER DRIFT. 1961. Breakdown of forest litter in relation to environmental factors. Plant Soil, 15: 295–311.

WOLFE, J. N., R. T. WAREHAM, and H. T. SCOFIELD. 1949. Microclimates and macroclimate of Neotoma, a small valley in central Ohio. Ohio Biol. Surv. Bull. 41: 1–169.